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THE ZOÖGEOGRAPHY OF NORTHWESTERNMOST SOUTH AMERICA (AFTER CHAPMAN)

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Modern botany and zoölogy, in their emphasis on ecology, or the environmental relation, rather than on the taxonomy, or classification, stressed by the older school of thought, closely approach the geographical viewpoint. Works composed from this standpoint therefore generally afford much of value and interest to the geographer. One of the most noteworthy among recent publications of this kind is Chapman's "Distribution of Bird Life in Colombia."¹ It is a report on an unusual biological survey—unusual, because its purpose, as the author states, was not to find new species of birds but mainly "the discovery of the geographic origin of South American life." The collections upon which the study is based were secured during a period of more than four years by expeditions from the American Museum of Natural History which were confined to the Andean region of Colombia.

The detailed notes on Colombian birds which form the bulk of the work (Part II, pp. 170–639) are preceded by introductory chapters illustrated by well-chosen photographs and maps (Part I, pp. 3–169). These chapters contain a review of the status of knowledge of Colombian ornithology, a general description of the routes followed on the Museum's eight expeditions, a summary of the topography, climate, and vegetation of the region, and—the culmination of the investigation—a discussion of the distribution of animal life in vertical "life zones" and its relation to the problem of the origin of South American life. This discussion, which consists of two parts, general conclusions (pp. 84–93) and individual characterizations of each life zone (pp. 93–169), is illustrated by the two colored maps which are reproduced in black and white herewith (Figs. 1 and 2).

THE VEGETATIONAL AREAS

Vegetation is recognized as the primary factor in animal distribution. Four types are distinguished, as follows (Fig. 1): mountain forests; tropical zone forests; unforested areas; and llanos. The dense tropical forests are clearly determined in the main by the low altitude, high temperature, and heavy rainfall. The lowland open areas are due to drought. The llanos are covered with tall grasses and scattered bushes and extend as strips along streams subject to much overflow. The arid regions of the upper valleys of the Magdalena and Cauca Rivers are, according to Hettner, due in part to a porous soil, to drought, and to high temperature. The upper Cauca valley has probably been cleared considerably. The mountain forests are

¹ F. M. Chapman: *The Distribution of Bird-Life in Colombia: A Contribution to a Biological Survey of South America*, *Bull. Amer. Museum of Nat. Hist.*, Vol. 36, 1917, pp. 1–729.

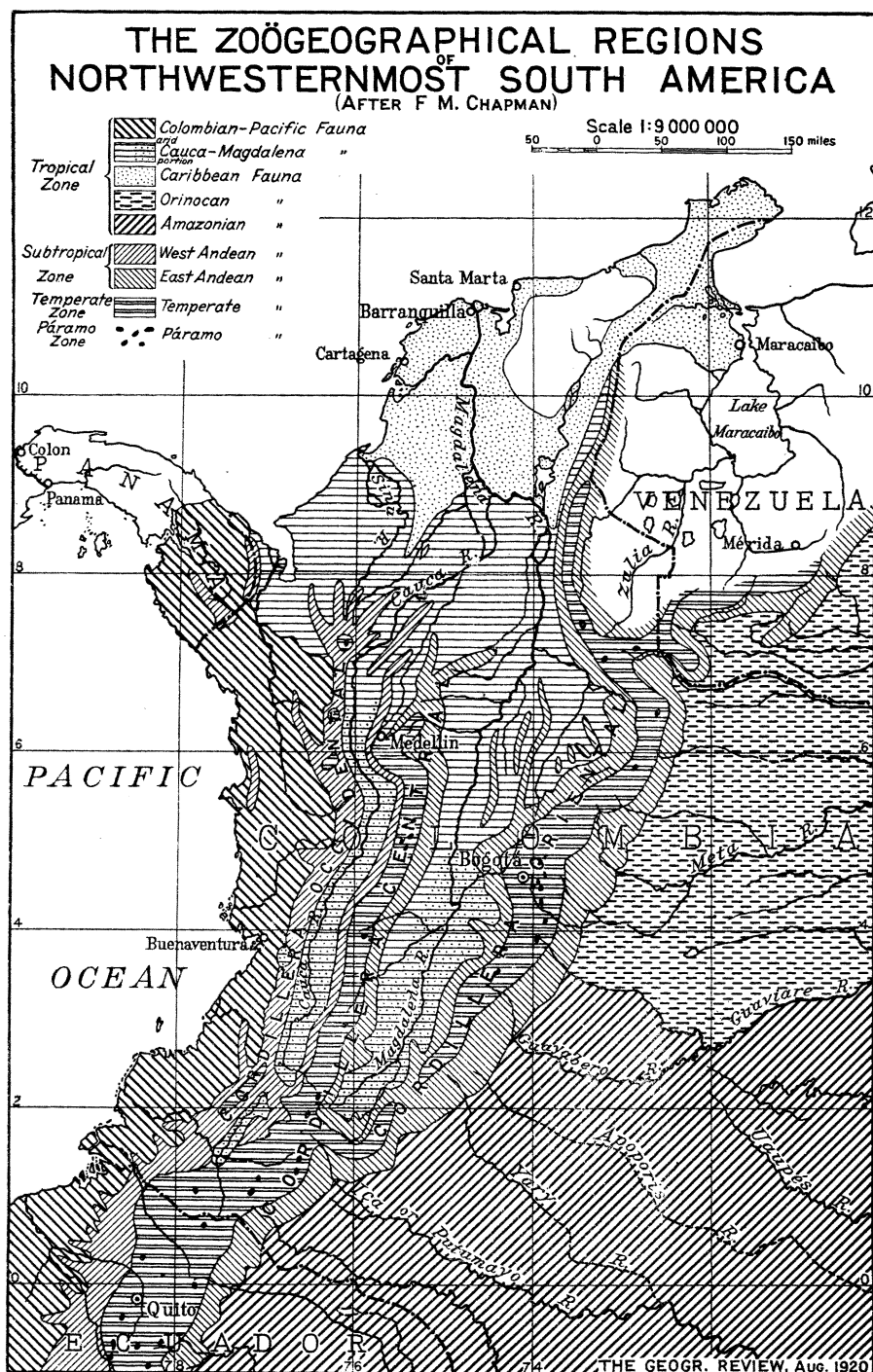


FIG. 2

subtropical and temperate in character and are cloud forests, their lower limit being determined by the altitude at which condensation takes place, while the upper limit of the temperate belt is coincident with the timber line.² The subtropical forests lie apparently between 5,000 and 9,500 feet. The lower forest is more continuous than the upper. The unforested mountains above the tropical zone are savana areas in the temperate zone, as also are those which extend above the temperate forests.

DISTINCTNESS OF THE LIFE ZONE BOUNDARIES

The discussion of the life, or faunal, zones of the Colombian Andes leads quickly to Chapman's main geographic interest and his main problem. He states: "That the altitudinal distribution of plants should conform closely to belts or zones, the limits of which are determined primarily by temperature, is not surprising; but that such mobile creatures as birds should be confined within certain more or less definite boundaries by these invisible barriers is a convincing evidence of their potency as well as of the sensitiveness of the organisms on which they act (p. 84) No one can stand at the foot of a snow-crowned mountain in the tropics without at once realizing that temperature, as it is influenced by altitude, is obviously the dominant factor in producing the floras and faunas encountered between base and summit. Where humidity, and in certain instances, character of the soil add their influence, the boundary lines between life zones are often very sharply defined. One may pass, for example, from the upper border of the arid tropics on the eastern slope of the Western Andes at San Antonio into the dense forests of the humid subtropics on their crest in less than two minutes and experience a complete change in bird life. But even where temperature alone is active, and there is no marked difference in rainfall, the forest being continuous, an altitudinal difference of 1,000 feet may bring one into an essentially new avifauna" (p. 84). "Even the condor, a sea-level bird of Patagonia, makes what we think of as his true home on the summits of the Northern Andes, where the factors which determine zonal boundaries keep him to his true level quite as effectively as they do a diminutive marsh wren" (p. 167).

ORIGIN OF THE PRESENT DISTRIBUTION OF ANIMAL LIFE

The birds show a distribution in four vertical life zones, as follows: tropical zone, sea level to 4,500–6,000 feet; subtropical, from 4,500–6,000 feet to 9,000–9,500 feet; temperate, from 9,000–9,500 to 11,000–13,000 feet; *páramo* (treeless), from 11,000–13,000 to snow line at 15,000 feet (Fig. 2). These zones are very similar to those recognized by students of plants. In order to explain these conditions Chapman makes a very significant remark, as follows: "Any attempt to explain existing conditions must be preceded by

² Some geographers and biologists do not seem familiar with recent ideas as to the causes of the timber line on mountains, so that reference is here made to the studies on this subject by Cowles and by Shaw (see *Amer. Naturalist*, Vol. 43, 1909, pp. 420–431; *Plant World*, Vol. 12, 1909, pp. 1–15); *Ecology*, Vol. 1, 1920, p. 71.

an effort to picture to ourselves the effect on the fauna of a tropical region of the uplift in it of a mountain system to snow line (p. 87) Where such an uplift created a mountain system as continuous as the Andes now are, these new areas were doubtless populated by latitudinal extension of range from regions having similar climates, and by altitudinal extension as the pressure of life from immediately contiguous regions below forced species upward, the more adaptable of which survived" (p. 88). He then considers successively the influence of elevation, glaciation, and subsidence. The Andean uplift, geologists believe, took place in the Tertiary, with additional uplift in the Pleistocene. With this background it is significant to note how these conditions have influenced the birds. Chapman remarks that the subtropical birds have been derived "almost wholly" from the zone below; the temperate from the subtropical, in part, as well as elsewhere from the same zone at sea level, "while nearly all those of the *páramo* zone have come from the sea level equivalent of this zone in southern South America. It follows, then, that the birds of every zone above the tropics have been derived from a lower level. There are some exceptions to this rule, but they do not affect the general truth of the statement. In comparative variability the fauna of the subtropics differs more from the ancestral stock in the tropics than do the altitudinal forms of the temperate and *páramo* zones from their distant sea-level derivatives of the south temperate zone, with which indeed they are often specifically identical. Hence it follows that uniformity of life increases with altitude while, as a corollary, the number of species decreases; uniformity of environment being apparently the underlying cause" (p. 88). These are indeed very important conclusions which should interest every geographer and student of earth history. They are probably the most important discoveries of the whole study.

It would be well worth while to apply these same methods to other parts of the world and to formulate a world-wide view of these biogeographic relations. The preceding quotation also suggests that the importance of habitat relations is even greater than the present study elaborates and shows that the relation of habitats to life zones is a subject worthy of detailed investigation.³ The kinds of birds decrease with altitude, in harmony with their simpler physical habitat. Chapman recognizes what he considers to be a Pacific coast pre-Andean tropical fauna (p. 89). On account of the former greater glacial activity on the Andes, he suggests that "existing zonal boundaries are post-glacial." As illustrating the influence of subsidence he cites the very interesting discontinuity of range of certain relatively sedentary subtropical birds occupying the mountains of Costa Rica and of

³ See Chas. C. Adams: Baseleveling and Its Faunal Significance, with Illustrations from Southeastern United States, *Amer. Naturalist*, Vol. 35, 1901, pp. 839-852.

Idem: Migration as a Factor in Evolution: Its Ecological Dynamics, *ibid.*, Vol. 52, 1918, pp. 465-490; Vol. 53, 1919, pp. 55-78.

Idem: An Outline of the Relations of Animals to Their Inland Environments, *Bull. Illinois State Laboratory of Nat. Hist.*, Vol. 11, 1915, pp. 1-32.

A. G. Ruthven: An Interpretation of the Distribution of the Reptiles in Maggie Basin, Nevada, *Bull. Amer. Geogr. Soc.*, Vol. 47, 1915, pp. 948-952.

Colombia, these birds being absent in the intervening lowlands of Panama, where subsidence is inferred. In concluding his discussion of the factors which influence life zones no mention is made of the vegetation, although elsewhere he repeatedly points out its influence upon birds. In fact in several particulars the logical development of his general discussion is not well worked out, and he does not seem to have been interested in the recent valuable methods of geographical description developed by W. M. Davis.

The Pacific coast tropical zone is quite unusual in many respects. It possesses great diversity in habitats, is very humid, and has been the main center of origin for Colombian birds. Finally, it is more strongly characterized than any other equal area of tropical South America, having about 150 species and subspecies. This is a very remarkable condition for a continental land mass. The relation of this fauna to that of the Amazon is also a distinctive feature, an affinity also shown by the Pacific-slope fresh-water fishes. There is evidence that one of the latest trans-Andean lines of faunal communication was in southern Ecuador. Another very significant geographical relation is shown in the Cauca valley, where but few kinds of birds are peculiar to the region. This fact suggested to Chapman that its fauna was a new one, and he suspected that the valley was the bed of an extinct lake. This idea is supported by White's geological evidence of a post-Tertiary lake in this valley caused by a volcanic dam.

In brief we may look upon the geographic origin of the bird fauna somewhat as follows: An elongated mountain range became elevated in the midst of a tropical region with a widely distributed Amazonian fauna and divided it. The Colombian Pacific tropical zone has now developed one of the most distinctive faunas found in the tropics on a continental land mass. As the mountains arose to a subtropical level a subtropical fauna was developed or evolved from the faunal stratum below. A part of this fauna was possibly destroyed by a depression in the Panama region, and a break in the continuity of range was made between the Colombian and the Costa Rican subtropical faunas, which at no point reached sea level. As the mountains continued to rise above the subtropical stratum and temperate conditions were developed, a direct continuity was established along the Andes (to the south) with the cooler lands near sea level, and a fauna migrated northward along the axis or backbone of the South American continent and mingled with that formed in place; later, as the alpine heights were reached, other invaders came from far south where they had been able to live at sea level. These alpine conditions were distinctly favorable during the period of alpine glaciers.

CONCLUSION

The many interesting and detailed distributional facts upon which these conclusions are based are discussed fully in pages 93-169, with tabulations and maps. The great bulk of the volume, as stated above, is devoted to the detailed notes on the numerous species of birds, and these notes are accompanied by several colored plates. A gazetteer of collecting stations

(pp. 640-656) contains information which is likely to be of value to many geographers as well as to bird students.

No one can read such an important and interesting volume without feeling the fascination of the problem and without hoping that the author may be permitted to extend his studies throughout the Andes. It may also be added that this is perhaps Dr. Chapman's most important contribution to zoölogy and to geography and will long remain a fine model for other students. Other naturalists and geographers will now become interested in testing his ideas. The bird population did not execute these migrations alone. The birds are dependent upon certain vegetational conditions and certain kinds of animal foods; and at the same time they would be followed by a predatory company, so that a whole biotic association must have traveled together and may be expected to furnish independent converging evidence on the origin of the South American fauna.